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Potential acoustic discrimination within boreal fish assemblages

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Differences in the acoustic characteristics of forage fish species in the Gulf of Alaska and the Bering Sea were examined using Kirchhoff ray-mode (KRM) backscatter models. Our goal was to identify species-specific characteristics and metrics that facilitate the discrimination of species using acoustic techniques. Five fish species were analyzed: capelin (*Mallotus villosus*), Pacific herring (*Clupea pallasii*), walleye pollock (*Theragra chalcogramma*), Atka mackerel (*Pleurogrammus monopterygius*), and eulachon (*Thaleichthys pacificus*). Backscatter amplitude differences exist among these species, especially between swimbladdered and non-swimbladdered fish. Echo intensities were variable within and among species. The effect of morphological variability was indexed using the ratio of the Reduced-scattering length (RSL) standard deviation over its mean. Morphological variability was low only at fish length to acoustic wavelength ratios less than eight. Target strength differences between pairs of carrier frequencies (ranging from 12 kHz to 200 kHz) differed among species, and were dependent on fish size and body orientation. Frequency differencing successfully discriminated between fish species but the choice of frequency to maximize target strength differences was not consistent among species pairs. Frequency-dependent, backscatter model predictions facilitate comparison of target strength differences prior to acoustic data collection.

Keywords: Bering Sea, forage fish, Gulf of Alaska, KRM model, species identification, target strength.

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Introduction

One of the main challenges and limitations in fisheries acoustics is species identification (Rose and Leggett, 1988; Horne, 2000; Petitgas *et al.*, 2003). The success of acoustic surveys to quantify and monitor marine populations depends on the accurate partitioning of echoes to constituent fish species. The discrimination of acoustic targets in mixed aggregations is particularly difficult and limits our ability to use echosounders as remote sensing tools.

Acoustic surveys are routinely conducted in the Bering Sea and the Gulf of Alaska to map walleye pollock (*Theragra chalcogramma*) abundance and document stock structure (Honkalehto *et al.*, 2002). Other forage species such as the capelin (*Mallotus villosus*), Pacific herring (*Clupea pallasii*), Atka mackerel (*Pleurogrammus monopterygius*), and eulachon (*Thaleichthys pacificus*) can be mixed with walleye pollock and complicate the interpretation of survey results. In many cases it may be impossible to partition acoustic energy to species based solely on the interpretation of sparse net samples. The acoustic information obtained from mixed aggregations is often dismissed because of our inability to properly identify or discriminate species.

The discrimination and identification of constituent species within acoustic data is accomplished using a variety of techniques. Typically these data are collected in conjunction with trawl samples to document species composition and length distributions in the geographic area of interest. The use of trawl-catch statistics to interpret acoustic samples has several limitations, including the selectivity and catch efficiency of the fishing gear among species, the resolution and paucity of net samples, and species partitioning and interpolation in non-sampled areas (Doonan *et al.*, 2003; O'Driscoll, 2003). Other approaches to identify targets use the direct interpretation and analysis of acoustic data. The discrimination and identification of fish species based on aggregation characteristics and image analysis metrics have been used (e.g. Weill *et al.*, 1993; Scalabrin *et al.*, 1996; Lawson *et al.*, 2001), but these techniques are limited when fish are dispersed. Alternatively, frequency-dependent backscatter techniques, such as mean volume backscatter differencing between two frequencies, have been used to separate broad species groups such as krill and swimbladdered fish (e.g. Kang *et al.*, 2002). Other methods, including discrimination based on echo-envelop metrics (e.g. Fleishman and Burwen, 2003) and broadband frequency spectrum (e.g. Simmonds *et al.*, 1996; Foote *et al.*, 1998) are promising, but these techniques are not mature. An alternative approach to species discrimination is the use of backscatter models to characterize the acoustic properties of fish (e.g. Clay and Horne, 1994; Horne and Clay, 1998). Kirchhoff approximations have been used to predict backscatter of several species, ranging from fish with large, air-filled swimbladders (Jech *et al.*, 1995; Horne *et al.*, 2000; Foote and Francis, 2002) to deepwater species without air-filled bladders (Barr, 2001; Kloser and Horne, 2003). Backscatter model predictions can be used to identify and isolate features among target types and the results can be used to determine the approaches that maximize species discrimination.

The main objective of this study is to examine whether forage fish species in the Gulf of Alaska and the Bering Sea have unique acoustic properties that would allow discrimination of single targets or groups of single targets with conventional split beam echosounders operating within the geometric scattering range. Using numerical models of acoustic backscatter, we evaluate several metrics for use in acoustic classification. Some constraints are identified and techniques to maximize detection are proposed.

Material and methods

We used a Kirchhoff ray-mode (KRM) backscatter model to characterize the acoustic properties of each fish species. Fish were captured at sea and radiographed to obtain lateral and dorsal images of the fish body and swimbladder. For species that do not possess a swimbladder, digital photographs were taken and used to trace the outlines of the body of the fish. These planar images were elliptically interpolated to render three-dimensional (3-D) representations of the fish bodies and swimbladders. The species analyzed were: capelin, Pacific herring, walleye pollock, Atka mackerel, and eulachon. If the sampled fish spanned a large length range, then the species concerned were partitioned into length groups. This reduced the morphometric variability within groups and limited the range of lengths at which fish were proportionately scaled during backscatter modelling (Table 1).

Each 3-D fish image was vertically divided in 1 mm thick, gas-filled (representing swimbladder) or fluid-filled (representing fish body) finite cylinders. Backscatter from each cylinder was estimated using the KRM model and then coherently summed to obtain backscatter estimates for the body, swimbladder, and whole fish (see Clay and Horne, 1994 for details). Scattering intensities are expressed as Reduced-scattering lengths (RSL, dimensionless), which is defined as the estimated scattering length ($\mathcal{L}$, units m, Medwin and Clay, 1998) normalized by the fish caudal length (L, units m). The absolute square of the scattering length gives the backscattering cross-section (σ_{bs}). RSL can be converted to target strength (TS, units dB):

Table 1. Species and length group used in the KRM backscatter models. The range indicates the minimum and maximum scaled length used in the models, centered approximately on the average (caudal) length of fish within each group.

Species	Range (cm) Min–[Mean]–Max	n	Swimbladder type
Capelin	10–[13]–20	34	Physostome
Pacific herring	10–[22]–30	30	Physostome
Walleye pollock	10–[14]–20	15	Physoclist
Walleye pollock	20–[26]–35	10	Physoclist
Walleye pollock	35–[42]–60	25	Physoclist
Atka mackerel	10–[18]–30	10	No swimbladder
Atka mackerel	30–[41]–50	10	No swimbladder
Eulachon	10–[17]–20	30	No swimbladder
Eulachon	20–[23]–30	13	No swimbladder

$$\begin{aligned} \mathrm{TS} &= 10\log_{10}(\sigma_{bs}) = 10\log_{10}(|\mathcal{L}|^2) \\ &= 20\log_{10}(\mathrm{RSL}\times\mathrm{L}) \\ &= 20\log_{10}(\mathrm{RSL}) + 20\log_{10}(\mathrm{L}). \end{aligned} \tag{1}$$

The target strengths of each species were compared over a wide range of lengths at frequencies corresponding to those commonly used in fisheries acoustics (12 kHz, 38 kHz, 120 kHz, and 200 kHz). Backscatter values were obtained by proportionately scaling each fish within a group over the same length range in the KRM model. Averages and standard deviation of backscattering intensities were calculated at each 1-mm interval. When averaged, scattering intensities were calculated in the linear domain prior to logarithmic transformation. All backscatter intensities were initially modelled at normal aspect (i.e. fish body perpendicular to the incident wave front). Ensemble target strength $\langle \mathrm{TS} \rangle$ is used to represent the mean echo intensity for a group at any specified length, tilt, and frequency. The KRM model predicts TS as a function of caudal length (i.e. tip of snout to end of caudal peduncle). To be consistent with other reported target strength to fish length relationships, caudal lengths were converted to total lengths (L_T) using linear regressions from collected specimens. Ordinal ranking of target strengths among species was compared across lengths and frequencies.

Variability within and among species was examined by calculating a coefficient of variation (CV = standard deviation/mean RSL) for a given species (or length group). To emphasize the influence and interaction of length and frequency in the potential for species discrimination, we plotted the inverse of the coefficient of variation (CV^{-1}) as a function of the ratio of fish length to acoustic wavelength. A low CV (or high CV^{-1}) within a group indicates low morphological variability. CVs were calculated for each species at normal aspect at 1-kHz bands over a frequency range of 12 kHz to 200 kHz. A CV was also calculated for each group at actual lengths, incorporating a normal distribution of tilt angles. For each group, 100 tilt angles were randomly generated from a Probability density function (PDF) based on published estimates of fish swimming angles (Figure 1). Backscatter values of every fish within a species or length group were estimated at each tilt angle and then averaged to obtain a tilt-averaged estimate. Tilt angles were restricted to ±40° from horizontal (dorsal aspect) to minimize the effects of extreme tilt angles (Reeder *et al.*, in press). CVs were plotted as a function of mean fish length and mean fish length to acoustic wavelength ratio at four acoustic frequencies (12 kHz, 38 kHz, 120 kHz, and 200 kHz).

Frequency-dependent backscatter was examined for each species by plotting target strength to total length ($TS-L_T$) relationships at several frequencies on the same plot. To facilitate comparisons, a series of arbitrary fish lengths (10 cm, 20 cm, and 50 cm) representing small, medium, and large fish were marked on the $TS-L_T$ function curves. Frequency-dependent backscattering characteristics were used to determine the potential for discrimination using target strength differencing. The difference in the predicted TS of individuals or groups of individuals was measured using pairs of carrier frequencies. This technique is comparable to the difference in mean volume backscattering strength (ΔMVBS) method (e.g. Madureira *et al.*, 1993; Kang *et al.*, 2002), in which the mean volume backscattering strength as a function of one frequency is subtracted from the mean volume backscattering strength of another (higher) frequency:

$$\Delta MVBS = MVBS(f_2) - MVBS(f_1), \qquad (2)$$

where MVBS is the mean volume-backscattering strength (logarithmic, units dB) and f_i is the frequency (kHz). In detailed form the equation is:

$$\Delta MVBS = \frac{1}{N}\sum_{1}^{N}\left[10\log_{10}\left(\frac{\sum\sigma_{bs}(f_2)}{V}\right)\right] - \frac{1}{N}\sum_{1}^{N}\left[10\log_{10}\left(\frac{\sum\sigma_{bs}(f_1)}{V}\right)\right]. \qquad (3)$$

where N represents the number of samples used to estimate MVBS, σ_{bs} are the backscattering cross-sections (m^2) of scatterers at each frequency (f_1 and f_2), and V is the volume ensonified. Assuming that individuals are randomly distributed within integration cells and are the same species and size (Kang *et al.*, 2002), or that sampling volumes are equivalent among transducers, we have:

$$\Delta MVBS = 10\log_{10}\left(\frac{n\times\sigma_{bs}(f_2)}{V}\right) - 10\log_{10}\left(\frac{n\times\sigma_{bs}(f_1)}{V}\right), \qquad (4)$$

where n is the number of individuals. By eliminating redundant terms (n: number of individuals and V: volume), the equation reduces to:

$$\Delta MVBS = 10\log_{10}\sigma_{bs}(f_2) - 10\log_{10}\sigma_{bs}(f_1), \qquad (5)$$

which is equivalent to:

$$\Delta TS = TS(f_2) - TS(f_1). \qquad (6)$$

ΔTS values were estimated using pairs of frequencies ranging from 12 kHz to 200 kHz. The technique was used to measure ⟨TS⟩ differences of fish groups modelled at normal incidence over a defined length range. The technique was also used to test differences in estimated TS of fish modelled at their actual length, and over 100 tilt angle values from the PDFs. The target strength mean difference for a given species or size group is calculated as:

$$\Delta TS_{f_2-f_1} = \frac{1}{m}\sum_{j=1}^{m}\left(\frac{\sum_{i=1}^{100}\left(TS(f_2)_{j,\theta_i} - TS(f_1)_{j,\theta_i}\right)}{100}\right), \qquad (7)$$

where m represents the number of individuals in a group, i is the number assigned to a random tilt angle value from the PDF (θ in degrees), and f denotes the frequency (kHz) used to estimate the target strength of individual j at tilt angle θ_i. Tilt-averaged ΔTS values from each fish were averaged to incorporate both the orientation and anatomical

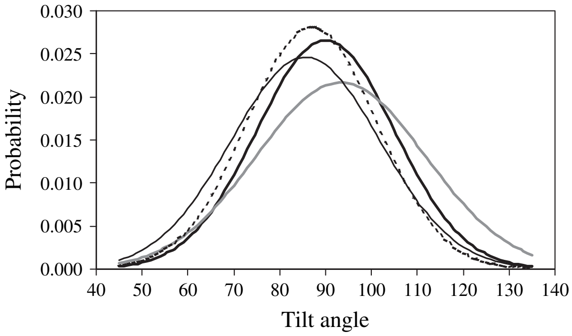

Figure 1. Tilt angle Probability density functions (PDF) used to estimate tilt-averaged target strengths. Dark grey line = capelin (Carscadden and Miller, 1980: mean = 93.3°, s.d. = 18.4°), broken line = Pacific herring (Ona, 2001, based on measurements on Atlantic herring: mean = 86.9°, s.d. = 14.2°), thin dark line = walleye pollock (Olsen, 1971, based on measurements on Atlantic cod: mean = 85.6°, s.d. = 16.2°), thick black line = Atka mackerel and eulachon (no published data: mean = 90°, s.d. = 15°).

variability of individuals within the species length group. Analyses of variance were used to detect differences among species (species "a" $\Delta TS_{f_2-f_1}$ – species "b" $\Delta TS_{f_2-f_1}$). When a statistical difference was found, *post hoc* analyses (Tukey's "Honestly Significantly Different" and Student–Newman–Keuls' tests) were performed to determine species-specific, pair-wise differences in ΔTS.

Results

Mean target strength (estimated at normal aspect) did not increase monotonically as a function of fish length (Figure 2). As expected, backscatter intensities of fish species without a swimbladder were much lower than any physostomous or physioclistous, swimbladdered species. Differences in echo intensity within swimbladdered or non-swimbladdered fish were not consistent across all lengths and frequencies. At 38 kHz, the ⟨TS⟩ of eulachon and Atka mackerel were much lower than fish with a swimbladder at all modelled lengths. At other frequencies, ⟨TS⟩ values for fish with and without a swimbladder were similar at opposite ends of the length range: the ⟨TS⟩ of large fish without a swimbladder was comparable to those of small fish with swimbladders.

Target strength variability increased with frequency. Ordinal ranking of echo intensity at 12 kHz was consistent at all lengths for species with swimbladders. Capelin had the lowest values, followed by walleye pollock, and Pacific herring. The ⟨TS⟩ of Atka mackerel appeared to be slightly higher than that of eulachon at the same length. At all the other frequencies tested, ordinal ranking among fish with or without swimbladders changed considerably throughout the modelled length range, with no consistent pattern or structure.

The coefficient of variation was explored as an index for potential species discrimination. At normal aspect, variability in echo intensity due to intra-specific morphological differences was low at fish length to acoustic wavelength (L/λ) ratios less than eight. The inverse of the coefficient of variation (CV^{-1}) emphasizes the potential for species discrimination at small L/λ ratios by increasing the range and scale of values (Figure 3). Mean coefficients of variation for fish measured at their actual length and over a PDF of tilt angles differed at 12 kHz (Figure 4). Atka mackerel and eulachon had the highest values (highest variability), followed by Pacific herring. Walleye pollock and capelin had the lowest values (lowest variability). Differentiation among swimbladdered species was not possible when splitting walleye pollock in length groups (roughly equivalent to juveniles, young adults, and mature fish). At higher frequencies (> 38 kHz), CVs were relatively high and discrimination among most species was impossible. Pacific herring had consistently higher values than the other species, indicating high levels of intra-specific morphological variability.

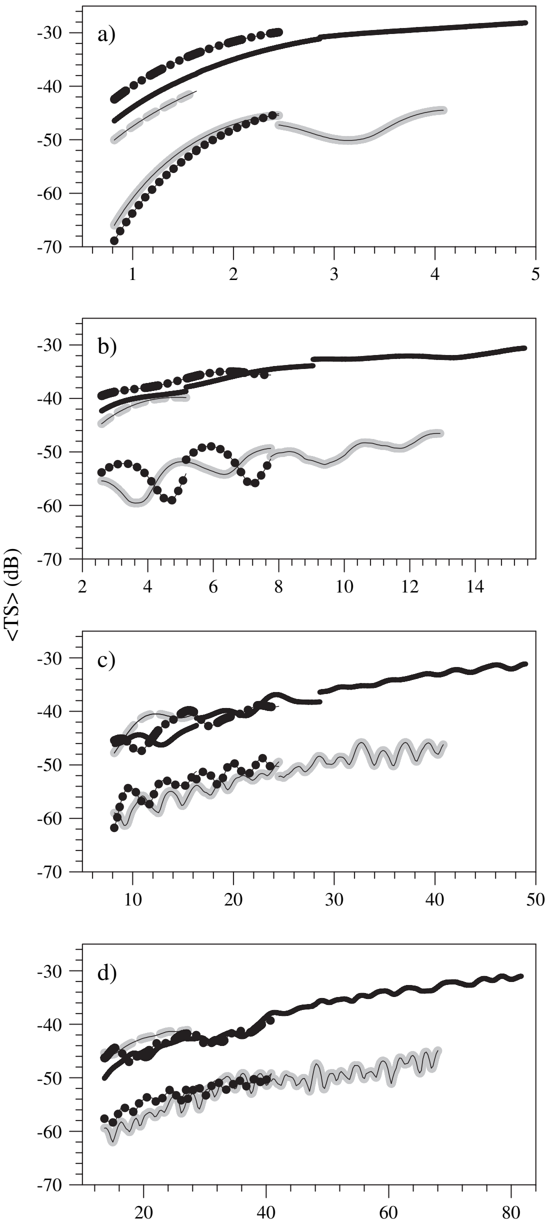

Figure 2. Mean target strength (dB) at normal aspect for the five species as a function of the ratio of fish length to acoustic wavelength (L/λ) at four discrete frequencies: (a) 12 kHz, (b) 38 kHz, (c) 120 kHz, and (d) 200 kHz. Modelled fish lengths range from 10 to 60 cm. Plotted curves are divided into sections when more than one length group is modelled for a species. Grey dashed line = capelin, black dashed and broken line = Pacific herring, black continuous line = walleye pollock, grey continuous line = Atka mackerel, black broken line = eulachon.

Frequency-dependent backscatter (within the geometric scattering range) appeared to be more prominent among small fish (Figure 5). For any given species, change in ⟨TS⟩ with frequency was greater for fish scaled to 10 cm than for

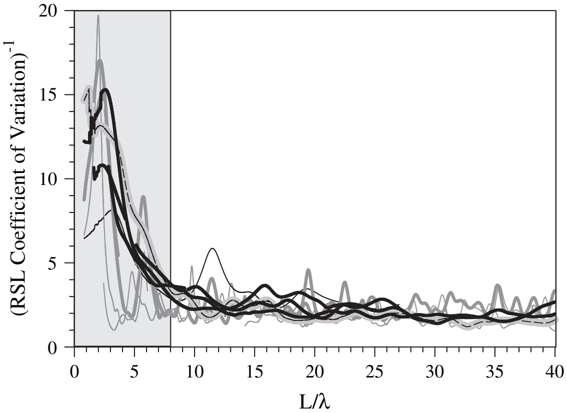

Figure 3. The inverse of the coefficient of variation (CV = standard deviation/mean RSL) as a function of the scaled fish length to acoustic wavelength ratio (L/λ) for all species and groups ensonified at normal aspect. Thin black line = capelin, dashed black line inside a grey line = Pacific herring, thick black line = walleye pollock (three length groups), thin grey line = Atka mackerel, thick grey line = eulachon (two length groups). CV $^{-1}$ values beyond L/λ of 40 are not shown and remain low (<5). The shaded box indicates $L/\lambda < 8$.

fish scaled to 20 cm or 50 cm. Amplitude and slope of the ⟨TS⟩ changes (increase or decrease) between consecutive frequencies were not consistent and depended on L/λ.

Dorsal aspect target strength differences (ΔTS) were most noticeable between 12 kHz and 200 kHz (Figure 6a). For 10 cm capelin, eulachon, and Atka mackerel, TS differences were high (positive values) and decreased rapidly with length. Values were the lowest for walleye pollock and Pacific herring. Differences in TS were also observed between 38 kHz and 120 kHz, but were not as high as the previous frequency pair (12 kHz and 200 kHz). Species rankings varied considerably across the modelled length range. Differences in TS were highly variable among non-swimbladdered species. For example, the ΔTS_{120-38} of eulachon varied by more than 15 dB over a length range of 20 cm. Target strength differences were lowest for walleye pollock and Pacific herring at this frequency pair, with the exception of a few nulls in eulachon and Atka mackerel values. Several successive ΔTS_{120-38} nulls and peaks could be observed for these species. Within the length range tested, capelin had consistently higher ΔTS values than for walleye pollock and Pacific herring (differences of 1 to 8 dB).

Target strength differences between carrier frequencies predicted for fish at their actual length and over a range of tilt angles yielded similar results (Figure 7). Mean differences in TS ranged from 1 to −11 dB (Table 2). Differences in TS were greater for fish with swimbladders. Species-specific ΔTS were significantly different at both the 200−12 kHz (ANOVA: $F_{4,171} = 151.9$, $p < 0.001$) and 120−38 kHz frequency differencing (ANOVA: $F_{4,171} = 97.8$, $p < 0.001$).

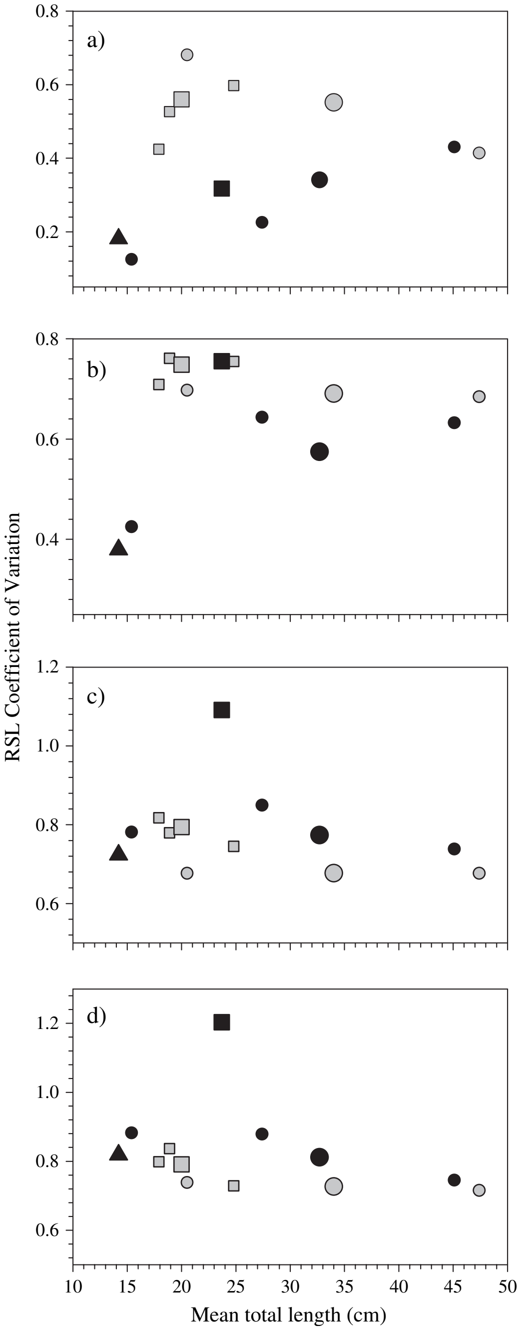

Figure 4. Tilt-averaged Reduced-scattering length (RSL) coefficient of variation (CV = standard deviation/mean RSL) as a function of the fish mean total length (cm) for all five species at four discrete frequencies: (a) 12 kHz, (b) 38 kHz, (c) 120 kHz, and (d) 200 kHz. Black triangle = capelin, black square = Pacific herring, black circle = walleye pollock, grey circle = Atka mackerel, grey square = eulachon. For species with more than one length group, the larger symbol indicates the mean value.

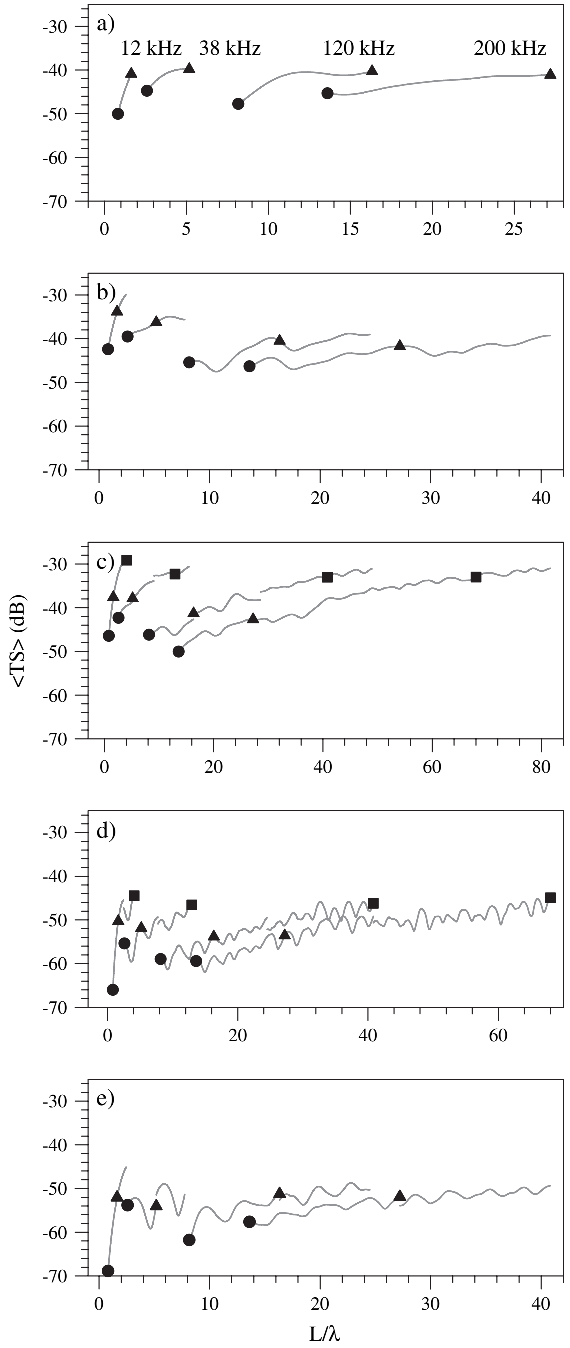

Figure 5. Dorsal aspect mean target strength to total-length relationships at four discrete frequencies (12 kHz, 38 kHz, 120 kHz, and 200 kHz) plotted as a function of the fish length to acoustic wavelength ratio (L/λ) for (a) capelin, (b) Pacific herring, (c) walleye pollock, (d) Atka mackerel, and (e) eulachon. For comparison across frequencies, a series of discrete fish total length were plotted: circle = 10 cm, triangle = 20 cm, square = 50 cm. Note L/λ ranges differ among plots.

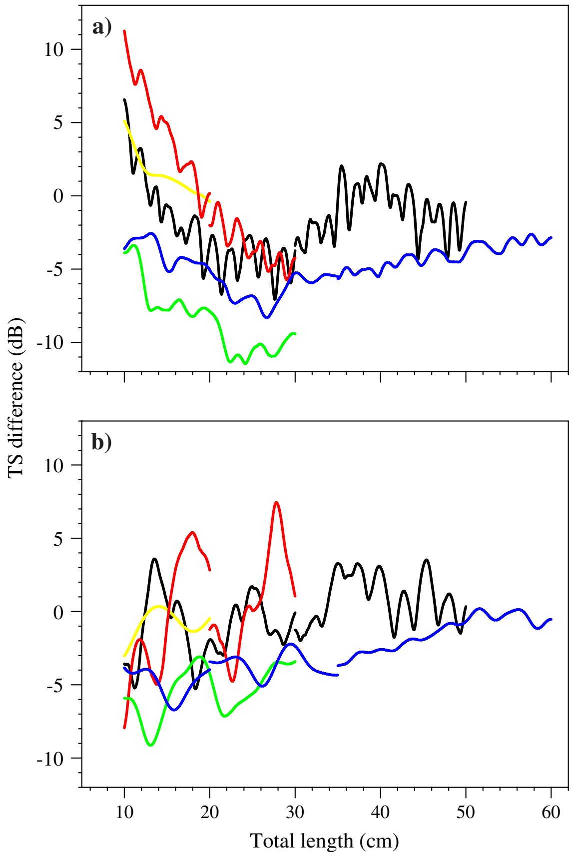

Figure 6. Target strength difference (ΔTS, units dB) for dorsal aspect mean TS measured over a range of lengths at (a) 200–12 kHz and (b) 120–38 kHz. Yellow = capelin, green = Pacific herring, blue = walleye pollock, black = Atka mackerel, red = eulachon.

Species-specific differences in TS differed between frequency pairs. Using 12 kHz and 200 kHz, Pacific herring had lower values than other species. Differences between capelin and walleye pollock were very small, especially at similar lengths. At the 120–38 kHz frequencies, capelin had the lowest average ΔTS, followed closely by Pacific herring. At these frequencies, fish that did not have a swimbladder had ΔTS_{120-38} values close to 0. Multiple comparison tests indicated that species could be separated in three target classes (c1–c3) based on ΔTS values (Table 3). Using 200 kHz and 12 kHz frequency differencing, the classes were (in increasing ΔTS order):

> [1: Pacific herring] > [2: capelin and walleye pollock] > [3: Atka mackerel and eulachon]

In comparison, the relative ranking of target classes using 38-kHz and 120-kHz frequencies was:

> [1: Pacific herring and capelin] > [2: walleye pollock] > [3: Atka mackerel and eulachon]

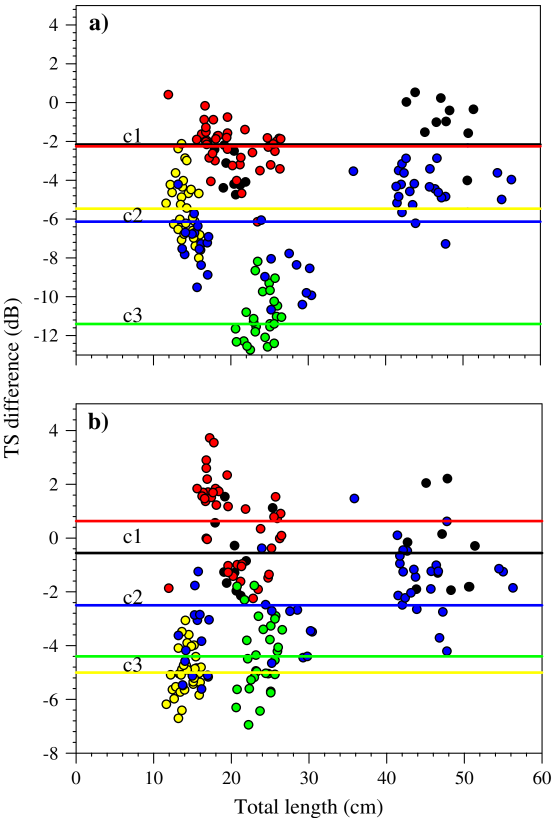

Figure 7. Target strength difference (ΔTS, units dB) for TS measured at (a) 200–12 kHz and (b) 120–38 kHz for each fish modelled at their default (actual) length and averaged over a tilt angle PDF. Significantly different classes of ΔTS are identified in both panels (c1–c3). Yellow = capelin, green = Pacific herring, blue = walleye pollock, black = Atka mackerel, red = eulachon. The horizontal line represents mean ΔTS for each species.

Table 2. Tilt-averaged TS mean difference (in dB) between combinations of carrier frequency [TS at 1st frequency (kHz) – TS at 2nd frequency (kHz)] for each species.

Capelin

1^{st} *f* (kHz)				2^{nd} *f*
200	120	70	38	
-1.4				120
-3.0	-1.6			70
-6.4	-5.0	-3.4		38
-5.5	-4.1	-2.4	1.0	12

Pacific herring

1^{st} *f* (kHz)				2^{nd} *f*
200	120	70	38	
-1.2				120
-2.6	-1.4			70
-5.6	-4.4	-3.0		38
-10.8	-9.6	-8.2	-5.2	12

Walleye pollock

1^{st} *f* (kHz)				2^{nd} *f*
200	120	70	38	
-0.5				120
-1.4	-0.9			70
-3.0	-2.5	-1.6		38
-6.1	-5.6	-4.7	-3.1	12

Atka mackerel

1^{st} *f* (kHz)				2^{nd} *f*
200	120	70	38	
-0.3				120
-0.2	0.2			70
-0.9	-0.6	-0.7		38
-2.2	-1.8	-2.0	-1.3	12

Eulachon

1^{st} *f* (kHz)				2^{nd} *f*
200	120	70	38	
-0.4				120
0.0	0.4			70
0.2	0.6	0.2		38
-2.3	-1.8	-2.2	-2.5	12

Discussion

One of the most promising techniques to discriminate species is target strength differencing. Our study is one of the first to examine potential target strength differences between several fish species having comparable length distributions and anatomical features. In previous studies, frequency-dependent scattering has been used to identify and discriminate krill and zooplankton from other scatterers such as fish (Cochrane *et al.*, 1991; Madureira *et al.*, 1993; Kang *et al.*, 2002). Kloser *et al.* (2002) successfully used frequency-dependent scattering with three frequencies (12 kHz, 38 kHz, and 120 kHz) to isolate echoes from different classes of scatterers: fish with large swimbladders (Macrourids and Mourids), fish with small swimbladders (Myctophids), and orange roughy (*Hoplostethus atlanticus*, a species with a wax-ester filled swimbladder). Using reverberation measurements in an echoic chamber, Conti and Demer (2003) showed potential differences in the scattering spectrum of sardine (*Sardinopps sagax caerulea*)

Table 3. Species-to-species comparisons of tilt-averaged, target strength differences (ΔTS) between carrier frequencies (f): species "a" $\Delta TS_{f_2-f_1}$ − species "b" $\Delta TS_{f_2-f_1}$.

		Mean difference (dB)	95% CI	
ΔTS_{200-12}				
Capelin	Pacific herring*	5.9	4.8	7.1
	Walleye pollock	0.7	−0.4	1.7
	Atka mackerel*	−3.3	−4.6	−2.0
	Eulachon*	−3.2	−4.3	−2.1
Pacific herring	Walleye pollock*	−5.3	−6.3	−4.2
	Atka mackerel*	−9.2	−10.6	−7.9
	Eulachon*	−9.2	−10.2	−8.0
Walleye pollock	Atka mackerel*	−4.0	−5.2	−2.8
	Eulachon*	−3.9	−4.8	−2.9
Atka mackerel	Eulachon	0.1	−1.2	1.3
ΔTS_{120-38}				
Capelin	Pacific herring	−0.6	−1.6	−0.4
	Walleye pollock*	−2.5	−3.4	−1.6
	Atka mackerel*	−4.4	−5.6	−3.3
	Eulachon*	−5.6	−6.5	−4.7
Pacific herring	Walleye pollock*	−1.9	−2.8	−1.0
	Atka mackerel*	−3.8	−5.0	−2.7
	Eulachon*	−5.0	−6.0	−4.1
Walleye pollock	Atka mackerel*	−1.9	−3.0	−0.9
	Eulachon*	−3.1	−4.0	−2.3
Atka mackerel	Eulachon	−1.2	−2.3	−0.1

*Asterisk indicates significant differences at the 0.01 level (Tukey's "Honestly Significantly Different" and Student−Newman−Keuls' multiple comparisons tests).

from that of anchovy (*Eugraulis mordax*) ensonified at frequencies ranging from 0.5 kHz to 202 kHz. Our model predictions suggest that it is possible to discriminate between species using combinations of two frequencies. Differences between any two species can be maximized using a particular combination of frequencies. For example, the ΔTS of capelin and Pacific herring are significantly different at the 200−12 kHz frequency pair, but not at the 120−38 kHz frequency pair. The inverse is true for the ΔTS of capelin and walleye pollock. Our results also indicate that target strength differences are dependent on fish size and body orientation. When individual targets can be resolved the first of these characteristics may not be a problem if the goal is to discriminate between species having different length distributions (e.g. small herring vs. large walleye pollock), or to discriminate between small and large individuals within a population (e.g. juvenile vs. adult fish). The same results could be obtained using ΔMVBS, as long as integration samples are small. In a mixed aggregation of fish having similar length distributions, target strength differencing might not discriminate species. The dependency of the technique on fish orientation further emphasizes the need for *in situ* observation of swimming behaviour and tilt angle distributions (Foote, 1980a; McQuinn and Winger, 2003; Stanton *et al.*, 2003). If orientations or sampling intensities differ among survey times or areas then MVBS or TS differencing values may vary.

Based solely on backscatter intensities at discrete frequencies, species could be separated in two functional groups depending on the presence or absence of a swimbladder. This is not surprising, since the swimbladder contributes to at least 90% of the sound scattered by a fish (Foote, 1980b). Within these two functional groups, backscatter model predictions for fish of the same length were very similar at all frequencies, with the possible exception of fish ensonified at 12 kHz. At this frequency, there was a consistent 3−4 dB difference among swimbladdered species. Unfortunately, the target strengths increased proportionately with fish length, which precluded unique TS values over a length range. Therefore, intensity differences would be confounded when species have overlapping length ranges which is often the case *in situ*. Fluctuations in TS over the modelled length range were more pronounced at higher length−wavelength ratios, thus reducing the efficacy of using differences in TS as a discriminatory metric.

The coefficient of variation reflects variability in TS due to morphological differences within a group of fish. Variation in body and swimbladder width, depth, and shape affect the amount of energy that is backscattered by a fish (Ona, 1990; Ona *et al.*, 2001). Using scaled fish lengths at dorsal aspect, our model predictions suggest that low variability occurs at low length−wavelength ratios ($L/\lambda < 8$). Differences in CV values among species vary, and depend on fish length and the frequency used to ensonify them. A more realistic model of *in situ* fish targets includes tilt, which also affects the amount of backscattered energy. Target strength is more sensitive to incident angle as frequency increases (Nakken and Olsen, 1977; Miyanohana *et al.*, 1990). High CV values are indicative of fish having high levels of morphological variability and a wide distribution of tilt angles or either property *per se*. The choice of a representative tilt angle distribution when estimating backscatter becomes crucial when interpreting TS variability. For walleye pollock, the CV appears to be sensitive to fish length, as illustrated by an increasing CV value across the three length groups at low frequencies. Ontogenic differences in body and swimbladder shapes may explain the differences observed in the CV metric (Horne, 2003). Our results suggest that differences in CVs are greater at low frequencies, which minimize the effect of tilt on target strength. Even though CV values among species have a larger range at low frequencies, the ability to discriminate species or length groups is limited.

Many factors affect the target strength of fish. Understanding the amount and source of TS variability is a challenge. A modelling approach offers the advantage of controlling and manipulating individual variables to examine their potential effect on TS over a range of conditions (e.g. Hazen and Horne, 2003). Such control is often impossible to achieve during *in situ* or experimental measurements. Model predictions from this study agree with empirical measures of target strength for the same or closely related fish species (Gauthier and Horne, in press). Backscatter model predictions can be used to quantify both the potential for and the constraints of species discrimination, and for recommendations on equipment configuration and analytic techniques to maximize acoustic detection.

Efforts to establish definitive acoustic species identification are not complete. Potential factors that have not been examined in this study include the effect of depth changes on the target strengths of gas-filled swimbladdered species (Gorska and Ona, 2003), and the inclusion of other scattering structures (e.g. backbone) in backscatter model predictions. Additional backscatter from other structures are not expected to be large, since the difference in acoustic impedance between cartilaginous bone and soft tissues is much less than that between gas in the swimbladder and flesh or bone (cf. Foote, 1980b). The integration of techniques may also increase the ability to separate species. Target strength differencing in combination with echogram imaging techniques (e.g. Korneliussen and Ona, 2003) and other discrimination tools such as aggregation metrics and neural networks (Woodd-Walker *et al.*, 2003) may provide a powerful means of discriminating between and the identification of fish species. Further efforts should be directed at the collection and analyses of *in situ* measurements of fish in mono- and multi-specific aggregations to test the metrics discussed in this paper.

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